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**PREFERENCE AND PERFORMANCE IN A POPULATION OF CHECKERSPOT BUTTERFLIES WITH KNOWN DIET HISTORY**

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**PREFERENCE AND PERFORMANCE IN A POPULATION OF**

**CHECKERSPOT BUTTERFLIES WITH KNOWN DIET HISTORY**


**by**

**Nur Hasanah, B.S.**


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# Dedication

This thesis is dedicated to my mother, who taught me that the best kind of knowledge to have is that which is learned for its own sake. It is also dedicated to my father who taught me that even the largest task can be accomplished if it is done one step at a time.

# Acknowledgements

I would like to thank Dr. Michael C. Singer for his invaluable guidance, support, and understanding in education and research as well as in life. I have never received such enormous encouragement, knowledge, and opportunities to experience from one person in my life. Without his understanding and support, it would be really difficult to achieve my educational goal in University of Texas at Austin. I would also to extend my gratitude to Dr. Camille Parmesan, Darcy McGillicuddy, and Sandy Monahan for their support and time and offering a great deal of patience, and indulging my curiosity. My sincere thanks are due to all members in Michael Singer's laboratory for their friendship, advice, and kind support, which made my experience in graduate school valuable. I would like to extend my gratitude to Dr. Damayanti Bukhori, Dr. Bandung Sahari, and Dr. Indarjani Komarudin for their continuous supported encouragement from Indonesia. It is always appreciated to have someone who longs for achievement in education and shares excitement about my research. My sincere gratitude is extended to my friends, Sabrina, Nichole, Yui, Kelsey, and Yeki, for their support through my experiment and sharing a lot of invaluable time and laughter, endless support, encouragement, and great love. I would like to thank the Ford Foundation for financial support, providing me an opportunity to have a higher education. Finally, I would like to thanks my father, Abdul Mufti, and my sister, Dewi Kurniawati for giving me this deep love and support.

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# Abstract

## PREFERENCE AND PERFORMANCE IN A POPULATION OF CHECKERSPOT BUTTERFLIES WITH KNOWN DIET HISTORY

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Abstract: This thesis describes a relationship between maternal preference and offspring performance in a population of the butterfly *Euphydryas editha* that used two host plants, *Pedicularis semibarbata and Collinsia torreyi* from 1979 to 2001, but now no longer uses *Collinsia*. In the light of the known history of diet change in this butterfly population, it is not surprising that maternal oviposition preference was variable. Although the diet of the butterflies that evolved rapidly in the 1980's is no longer changing, I still discovered some females with a chemical preference for *Collinsia*. This seems to be a legacy of recent anthropogenic diet evolution. The evolution of host preference of females in Rabbit Meadow has not finished yet. Variation of offspring weight and survival were measured and showed a complex relationship with adult preference. Although quite a few adults strongly rejected *Collinsia*, their offspring grew well on this host, and there was no significant trend for the offspring of strongly *Pedicularis*-preferring butterflies to perform more poorly on *Collinsia*.

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# Chapter 1: Introduction

The importance of interaction between plants and animals has long been well known. In the late archean and early proterozoic, micro-paleontologists have successfully identified fossils of photosynthetic microorganisms' and bacteria that provide the first evidence of animal-plant interaction (Flores et al 2009). In the 18$^{th}$ century, Charles Darwin described in detail the complex web of animal-plant interactions (Darwin, 1859). He observed the association of plants and their pollinators and the remarkable adaptations in the structure and behavior of plants and animals that make pollination processes so effective. Hairston et al, in1960, started studying plants and their relationships with herbivores in the context of ecological community theory, and the terms of ''top-down" and ''bottom-up'' effects arose to describe the interaction between consumers and their resources, such as, between predator and prey, and between plant and herbivore.

Today, the studies of interactions between plants and animals are well-developed, including those between herbivorous insects and their hosts. For example, an herbivorous insect may select for oviposition a particular species, a particular genotype, an individual genotype in a particular site, and even a particular canopy level in a forest.

One way to understand the ecology and evolution of the plant-insect interaction is to study how mother's oviposition preferences relate to offspring performance (Rausher 1982, Thompson, 1988). Some people such as Wiklund, (1975), Chew, (1977), Jaenike (1978), and Mayhew (1998) make predictions of this relationship for example, that mother's preference should be correlated with offspring performance. Mayhew (1997) suggested that a female is expected to choose a host to oviposit on which her larvae perform the best. The oviposition site that mother prefers could influence different aspects of offspring performance, such as offspring fecundity, survival to reach adulthood, and size (Rausher 1979). However, the maternal preferences of individual females are variable among species and even within a single population, which may also influence their offspring's' performance. Observations show that females do not always choose plants on which offspring performance is high. A positive correlation is shown in some studies, such as those by Ng (1998) and Eben et al (2000). In contrast, Cronin & Abrahamson (2000) studied the relationship between female habitat preference and juvenile survival. They found that the female's habitat preference does not always favor the best place for their offspring's' development. Rausher (1979) and Craig et al (1999) likewise failed to find positive correlations between habitat choice and offspring performance.

Maternal host preference is not only influenced by ecological pressure, for example by time (Rausher, 1978), Singer (1982), Janz and Nylin (1997), enemy free space, and patch dynamics, but also by the genotypes of the females (Thompson, 1988). In other words, ecological factors are not enough to predict preference-performance correlations. Doak et al (2006) predicted that females that have few eggs with plenty of time would be picky about oviposition sites. Meaning, that each egg is a major component of a female's potential fitness, and she has both the need and the time to choose carefully.

The definitions of “preference” and “performance” are quite diverse (Singer 1986; 2000; 2004) and may depend on the question being asked (Thompson, 1988). I will use “preference” as an individual behavior that causes plant A to be chosen over plant B in terms of ovipositing and/or feeding (Singer, 1986; 2000; 2004). When a female is offered plants, she may express preference by ranking them (Singer and Lee, 2000). A “performance” is defined by Thompson (1988) as a measure of offspring survival, development (weight), or fitness. In this thesis, I will use offspring larval weight as a measure of offspring performance.

The butterfly *Euphydryas editha* is an herbivorous insect in which it is feasible to examine the maternal preference-offspring performance relationship. Its host plants are *Penstemon, Castilleja Collinsia, Plantago,* and *Pedicularis*. Singer (1994) recorded how eggs were placed in different hosts in 37 different populations of the butterfly. Some of the populations were truly monophagous and some were not, meaning that in some places, they had minor hosts in their diet, (Singer, 1983).

*E. editha* lives in parts of California, including Rabbit Meadow, Seqouia National Park, where its hosts *Collinsia* and *Pedicularis* exist. They have an interesting life. The butterflies used to oviposit on *Pedicularis semibarbata* as their traditional host plant, but Singer (1983) concluded that since 1967, their diet had changed dramatically after clear cut and burn performed by the US. Forest Service. After clear cut and the burning, the butterflies began to oviposit on a novel host plant, *Collinsia torreyi,* that was growing in the clear cut-burned area. They still used *Pedicularis* in the undisturbed area. However, after couple of decades, although *Collinsia* is still abundant, the numbers of adults that prefer *Pedicularis* are higher than numbers that prefer *Collinsia* (Thomas & Singer (1987), Singer et al. (1992, 1993), Parmesan et al. (1995)). In addition, after 2002, Singer (pers. com) did not find any *E. editha* that preferred *Collinsia.*

In the light of the known history of diet change in this butterfly population, in this thesis I would like to present: First, current variation of maternal oviposition preference. Second, I will also report the correlation between mother's preference and offspring growth. Finally, I will report the relationship between offspring survival and mother's preference. This study will contribute to understanding the evolutionary ecology of animal-plant interactions, especially in conditions where those interactions are rapidly-evolving.

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# Chapter 2: Literature review

Interactions between animals and plants have existed for 450 million years (Labandeira 2002). These interactions can take the form of mutualism, parasitism or, when an insect consumes an entire plant, predation. In addition, ecological and morphological data, such as functional feeding groups, dietary guilds and mouthpart types are very useful to provide the history of insect-plant interactions and ecological differentiation in time and space.

#### HOST SELECTION AND OVIPOSITION BEHAVIOR BY ADULT FEMALE

Host plant selection, which is performed by females when ovipositing, is not a simple process. Insects make specific behavioral responses in host selection (Kennedy, 1965).

Many researchers state that host selection by females serves to optimize offspring development and mother's fitness. Awmak and Leather (2002) wrote that if a female selects a low quality plant; offspring would take longer to develop. For this reason the mother is predicted to choose good quality plants to oviposit. The quality of host plants can depend on nutrients and secondary chemicals (Renwick 2001), physical characteristics such as leaf size and texture (Miller and Strickler 1984, Harris and Miller 1988), host damage, host age, host abundance, density, diversity, and also the existence of vegetation around host plants. In addition, offspring fitness on a plant is affected by the plant's association with natural enemies (Thompson, 1988). We might expect oviposition choice to respond to this, and Sadek et al. (2006) found that *Spodoptera* *littoralis* chose for oviposition individual leaves on which parasitoid attack was least likely. However, each individual can have different responses to host plants.

The selection of host plants by females also depends on effects of time (Thompson 1988). Papaj and Rausher (1983) defined this time effect as “the changes in responsiveness in relation to time elapsed since the insect last fed or oviposited”. Some females will take a long time to search for host plants before deciding to oviposit and different insect species typically search for different lengths of time. In addition, different species express high specificity at different stages in the host selection process. *Euphydryas editha* has three steps of behavior before deciding (Parmesan et al. 1995), aphids also have three behavioral stages when selecting a host plant (Powel et al. 2006).

To select a host plant, insects use sensory clues such as visual, olfactory, gustatory, tactile stimuli, humidity, and also light intensity (Bernays and Chapman 1994). The decision to oviposit often involves evaluating a combination of many stimulatory and inhibitory plant chemicals acting together. A large number of sensory receptors of different modalities receive stimulation at each step in the host selection process. This information must be processed and integrated by the central nervous system, interpreted as a positive or negative signal and a decision made as to whether to make a certain behavioral response (Hanson 1983, Schoni et al. 1987).

Oviposition behavior is a principal mechanism by which the insect host relationship is established (Singer 2004). The relative immobility of offspring in most Lepidoptera assigns host selection for larvae as the responsibility of the ovipositing female (Singer 1986). Thus, the selected site of oviposition that is chosen by female is crucial. It can influence all aspects of larval performance (Resetarists 1993).

### THE DEFINITION OF "PREFERENCE" AND "PERFORMANCE" TERM

There has been confusion about what exactly the definitions of preference and performance should be. The definition of "preference" is variable. It depends on what question we ask. Here, I will use a definition of "preference" as a behavioral trait. A "preference" is expressed when, given a choice between two host plants, A and B; the individual will select A over B or B over A. Individuals with different levels of motivation will also have different responses to the same plants (Singer 1986, 2000). The meaning of "preference" sometimes is hard to distinguish from "acceptance" (Singer et al 1992). "Preference" will be hard to assess in the field accurately because its definition involves comparing responses to plants that are encountered simultaneously, yet such encounters do not happen simultaneously in nature. Simultaneous encounters probably cannot even be arranged with captive insects. However, we can approach this ideal situation by making observations in a preference experiment (Mayhew 1997).

The word "Performance" refers to offspring growth rate and survival rate. Growth rate can be measured by weight after a standard length of time (Ng 1988, Thompson 1988).

In my research, I use the term "preference" to describe female oviposition behavior in accepting some plants and rejecting others. My measure of "performance" is offspring weight and survival.

## EUPHYDRYAS EDITHA PROFILE

### Taxonomy

Edith's checkerspot (*Euphydryas editha*) is a medium-sized (winglength 1.5-3cm) Nymphalid butterfly. Its colors are red-orange, yellow and black or brown.

### Ecology and Development

*E. editha* are univoltine, usually flying in summer after snowmelt (Murphy et al., 2004). They drink nectar from flowers of a variety of annual and perennial plants.

The female will lay eggs in clusters of 1-350. They hatch in 13-15 days. The~~ir~~ larvae feed on a taxonomically restricted set of hosts. The development of the prediapause larvae has three instars, taking 10-14 days. Usually when they molt into the fourth instar they enter diapause. This typically happens in summer when their host plants start to senescence. Before the host plants senesce, the prediapuse larvae are in a race to reach diapause (Singer, 1972). However, specifically for Bay Checkerspot (*E. editha bayensis*), the percentage of the mortality of pre-diapause larvae is high, it is usually only around 1 % that survives (White 1974), the survival rate depending on the availability of green and edible host plants. Working in the same population of *E. editha* that is the subject of the current study, Moore (1989) reported that survival to diapause of second-instar larvae was 31% on Collinsia, and 19% on *Pedicularis*. Starting in the first instar larvae usually live in a silken web on the host plant that their mother selected. On some hosts, such as *Pedicularis,* it is hard for larvae to survive if they are not in a large group in their web. In contrast, on other hosts, such as *Collinsia*, larvae survive better in smaller groups (McBride & Singer 2010).

## Behavior

### *General*

*Euphydryas editha* fly low to the ground, in straight lines or zigzag, and their variegated wing patterns may make it difficult for natural predators to follow them when they are flying. The adults feed on nectar of flowers, usually with their wings open.

Because has a limited time, sometimes, a female insect chooses a poor quality plant to oviposition on. She should decide quickly and not spend a lot of time to assess the quality of hosts when she could otherwise be searching for a new host.

### *Searching for host plants*

Before laying eggs, females of *Euphydryas editha* will investigate different plants and sites using both pre-alighting and post-alighting components of behavior. If the search continues to the end of the discrimination phase, then the low-ranked host can be accepted. In fact the average length of search is more like 30 minutes for *Pedicularis*-feeding insects and maybe 3-10 mins for *Collinsia*-feeders that oviposit many times per day (Singer 1982). We can recognize whether they accept or reject the plants by observing their post-alighting behavior. A female assesses a plant by dipping her antennae, flapping her wings, and extending her fore tarsi to tap the surface of the plant several times (Singer 1982, Parmesan et al. 1995). If she accepts a plant, she will curl her abdomen and prepare to lay eggs, but if she leaves the plant, this is recognized as a rejection (Singer 1982). In addition, Mackay (1985) reported that *Euphydryas editha* generally has time to discriminate among plants. Their discrimination time takes much longer than in most butterflies. The average time for a single oviposition search by *E. editha* is on the order of 30 minutes.

In Rabbit Meadow, Sequoia National Forest, California, the alighting that is done by *Euphydryas editha* is principally a response to visual stimuli (Parmesan et al. 1995). This assumption was shown by the strong relationship between alighting bias and plant visual traits.

**Euphydryas editha's host plants**

*Euphydryas editha* as a species has multiple host plants at sites in California, such as *Castilleja, Plantago*, *Penstemon*, *Pedicularis*, *Collinsia,* and *Mimulus*. The interesting thing is at each location and in each habitat; the butterfly has different host plants. For example, *Euphydryas editha* at San Fransisco Bay, oviposits on *Plantago*, while at Frenchman Lake Singer & Parmesan (1993) found 20-30 clusters on *Penstemon*, and only one cluster on *Collinsia*. In Rabbit Meadow, *Euphydryas editha* oviposits on *Pedicularis, Castilleja*, and *Collinsia*.

*Pedicularis semibarbata* and *Collinsia torreyi* are native plants in California and Nevada. *Pedicularis* is perennial, while *Collinsia* is an annual herb that can be found near coniferous forests. *Pedicularis semibarbata* , which has a common name as pinewoods lousewort, produces leaves which are about 20 centimenters long. Most of them lie close to the ground in a rosette. *Collinsia torreyi,* which is known as Torrey's blue-eyed Mary, is a species from the plantain family. The height of the plant is around 25 centimeters, and it produces reddish stems. When using *C.torreyi,* the different life stages of the insect feed on phenologically different plants. Old larvae will eat seedlings, which are germinating, and the young larvae of the next generation feed on the senescing plants.

**The history of host plant preference of *Euphydryas editha* in Rabbit Meadow**

The host plant preference of *Euphydryas editha* females at Rabbit Meadow has been quite variable over time. In the past, they used *Pedicularis semibarbata* as their host plant. However, this changed when the US Forest Service clear cut and burned the area, where the plants grew. These activities caused the *Pedicularis* to die. After the anthropogenic disturbance, most of the butterflies used *Collinsia* as their host plant in the clear cut and burned areas, while they still used *Pedicularis semibarbata* in undisturbed areas (Singer 1983).

The anthropogenic disturbance caused evolution of *Euphydryas editha*. This process is quite fast (Singer et al. 2007). The proportion of individuals that preferred *Pedicularis* and *Collinsia* fluctuated over time. In the years 1979-1981, butterflies that preferred *Pedicularis* were more frequent than those that were *Collinsia*-preferring, In 1989, the numbers of individuals that preferred *Pedicularis* and *Collinsia* were the same (Singer & Thomas 1996). However the data from 1982 to 1986 showed that there were more larvae that fed on *Collinsia*, but the frequency of *Pedicularis* preference was higher than that of butterflies that preferred *Collinsia* (Singer et al. 1993) From 1999 through the 2000s, *Collinsia* has hardly been used at all by the butterfly population (Singer et al 2007).

# Chapter 3: Maternal Preference and Offspring Performance of *Euphydryas editha*

## INTRODUCTION

Studies of maternal preference and offspring performance relationship have been done to help understand the ecology and evolution of animal-plant interactions. The review paper that was written by Mayhew (1997) is surprising, because the finding of positive relationships is rare. He compared studies that found negative correlations and those which found positive correlations between maternal preference and offspring performance. Some studies failed to find any correlation.

As a prediction from evolutionary theory, generally we expect positive correlations between maternal preference and offspring performance (Jaenike 1978, Leather 1994). Among the investigations result in a positive relationship are those by Wiklund (1975), Rausher (1982), Thompson (1983), Singer (1984), Nylin and Janz (1993), and Poykko (2006).

However, some empirical data also show poor correlations (Courtney and Kibota 1990, Mayhew (1997), Aurbach and Simberloff (1989), Fox & Eisenbach (1992), Singer et al. (1994), Berdegue et al. (1998), Jallow and Zalucki (2003), Rajapakse and Walter (2007), Ishihara (2007).

The different findings in these studies may be because host choice and larval performance are variable, depending on ecological conditions and selection pressure (Thompson, 1988). Poor correlations could be caused by the effect of differences quality of food quality or even by human error (investigator) (Thompson and Pellmyr 1991).

Many organisms have been used to measure the correlation of maternal preference and offspring performance, including my own study species*,* *Euphydryas editha*. Singer (1971) is the first person who started asking why and how *E. editha* discriminate among their host plants. Additional studies of maternal preference have been done by Singer (1983), Thomas & Singer (1987), Ng (1988), Singer et al (1991, 1992)~~,~~ and Singer and Parmesan (1993).

*E. editha* at Rabbit Meadow discriminate among individual *Pedicularis semibarbata* within a single species.  Ng (1988) reported a correlation between preferences of females for individual *Pedicularis semibarbata* and their offspring survival. It seems that every individual in this species has a different motivation (Singer et al 1992). Evolutionary changes of the host preference of *E. editha* can be fast (Singer et al. 1993). This was especially true in Rabbit Meadow, where the US Forest Service clear-cut and burned patches where *Pedicularis semibarbata* were abundant. After the anthropogenic disturbance, *Euphydryas editha* used *Collinsia torreyi* in burned areas and *Pedicularis* in undisturbed areas.  It is interesting to investigate these phenomena again after decades have passed.

Hence, this current study was conducted to test the current variation in host preference~~s~~ of females at Rabbit Meadow and to ask whether there is a correlation between female preference and offspring performance.

## MATERIAL AND METHODS

### General

I obtained *Euphydryas editha* randomly from nature in Rabbit Meadow, California, at an elevation of 2300 meters. The traditional host plant of *Euphydryas editha* in Rabbit Meadow is *Pedicularis,* and the novel plant is *Collinsia.* I captured the butterflies June-July, the time when they were flying after snowmelt. I arranged matings for virgin females, and I did not mate them if they were not virgin. Before I did the oviposition test, I tested each female on *Pedicularis semibarbata* to examine whether they were ready to lay eggs or not. This was done to avoid motivational state interfering with measurement of preference.

### Measuring variation of maternal preference

Forty individuals of *Euphydryas editha* were tested on their traditional plant, *Pedicularis semibarbata*, and their novel plant, *Collinsia torreyi*, in a behavioral test of oviposition preference.

For investigating oviposition preference ranking by females, I categorize the behavior into four categories (MC Singer pers.com), they are:

1) No Preference (N), when the first acceptance of each host occurs in consecutive encounters.
2) Preferring *Collinsia* (C), when a female accepts *Collinsia* and subsequently rejects *Pedicularis.*
3) Prefer *Pedicularis* (P1), when a female prefers *Pedicularis* but accepts *Collinsia* on the same day.

4) Prefer *Pedicularis* (P2), when a female accepts *Pedicularis* and rejects *Collinsia* late on the day when *Pedicularis* is first accepted
5) Prefer *Pedicularis* (P3), when a female accepts *Pedicularis* on day 1 and still rejects *Collinsia* late on day 2.

"Acceptance" here is defined as a female curling her abdomen (Singer, 2004), while "Rejection" is defined as female not curling her abdomen at all during a five-minute test.

To test whether females were motivated to lay eggs or not, I tested them by putting them on their traditional host plant~~s~~, *Pedicularis semibarbata* before doing the behavioral preference test. It was for avoiding for motivational state of the individual. If a female was motivated, and curled its abdomen within 5 minutes, then I would not use it, in order to avoid confounding effects of motivation and preference,

After testing the females on *Pedicularis*, I started to test them for behavioral preference. I put the individuals gently on the plants. For example, I put female number 1 on *Collinsia* first, and waited five minutes for her to respond. Either she rejected or accepted the *Collinsia*. After five minutes, I removed her, placed her on *Pedicularis* and again waited five minutes for her to respond. If a female accepted a plant, and prepared to lay eggs, I did not allow her to oviposit before finishing the test and recording her responses to the plants. The interval between each sequence was 20 minutes. A butterfly that accepted one plant and rejected the other was re-tested until she accepted both plants or until the end of the second day of testing.

### OFFSPRING PERFORMANCE

After they laid eggs on the host plants that they preferred, I removed the eggs from the each cluster to a small vial. I separated 10 eggs from each cluster and marked each group with their mother's identity number and preference. The weight of the larvae and the survival were recorded, and used as estimates of "offspring performance."

## Chapter 4: Oviposition preference of females's *Euphydryas editha* at Rabbit Meadow

### VARIATION OF E.EDITHA FEMALE ADULT PREFERENCE AT RABBIT MEADOW

Adult females of *E editha* at Rabbit Meadow are quite variable in their oviposition preferences (fig 1). Among the 40 female adults of *E. editha* that I tested, the largest category comprising thirteen individuals, accepted *Pedicularis* and *Collinsia* equally (N). In contrast, only three individuals preferred *Collinsia*, rejecting *Pedicularis* after accepting *Collinsia*. These individuals are categorized as C.

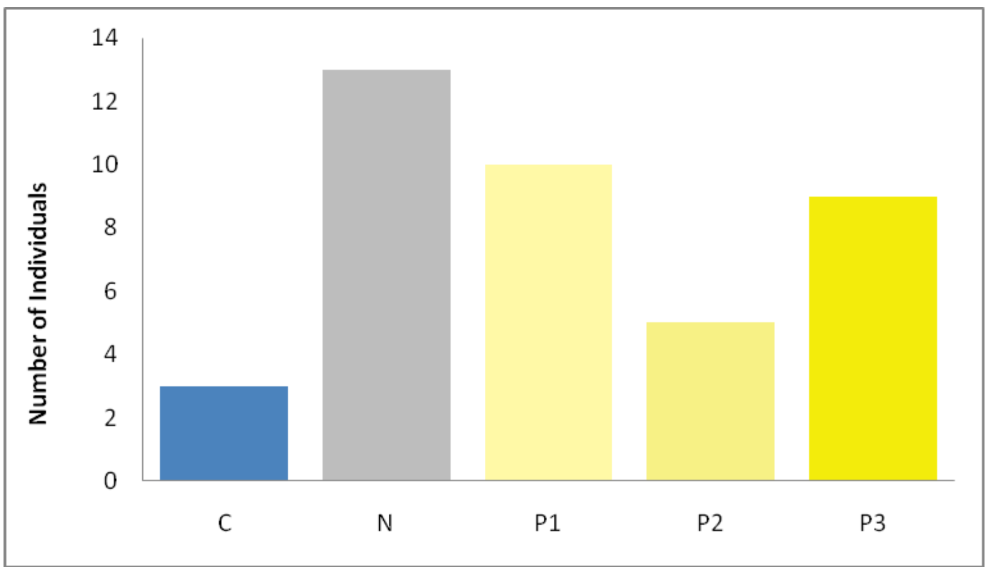


Figure 1: The proportion of mothers with each oviposition preference.

Ten females that I placed in category P1, with weak preference for *Pedicularis*, preferred *Pedicularis* but accepted *Collinsia* on the same day. Only five individuals were in category P2, preferring *Pedicularis* and rejecting *Collinsia* at the end of day 1 but accepting *Collinsia* on day 2. Category P3 comprised nine individuals that preferred *Pedicularis* strongly, and still rejected *Collinsia* at the end of day 2 .

### MOTHER PREFERENCE VS. OFFSPRING SURVIVAL

The overall survival of offspring from mothers in each preference class is shown in figure 2. The trend was for higher survival among offspring of butterflies without preference (N).

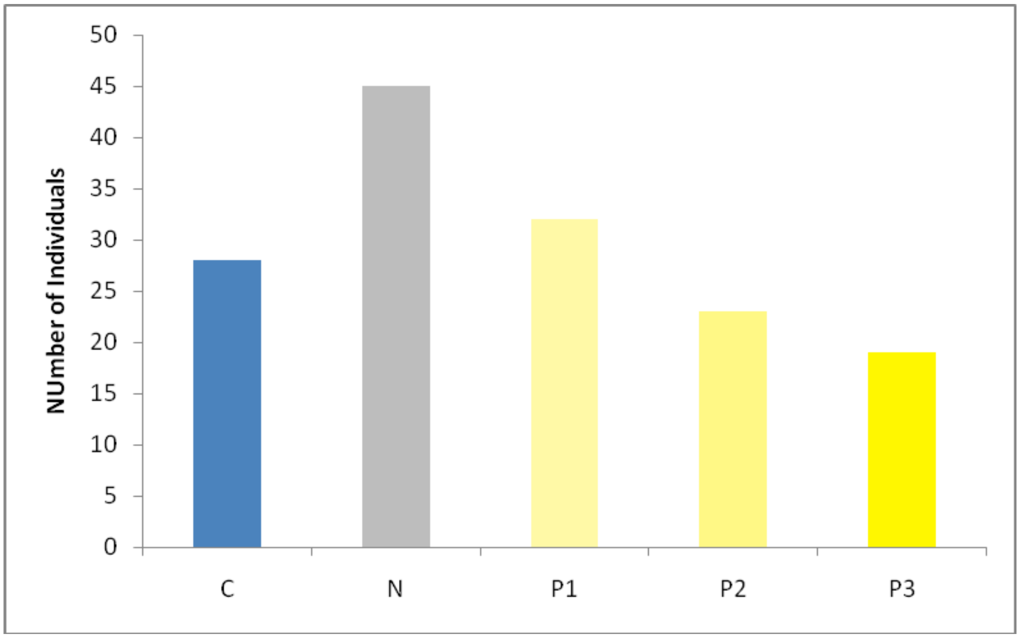


Figure 2: Maternal preference and offspring survival

### MOTHER PREFERENCE AND OFFSPRING WEIGHT

The theory of optimal oviposition by Jaenike (1978) predicts a positive relationship between mother's preference and offspring performance. Offspring performance was recorded by measuring the mean weight of the larvae (figure 3). The figure shows the total weight of offspring in different maternal preference categories on *Pedicularis* and *Collinsia*. The mean larvae weight from N and P2 mothers is shown as the heaviest. In contrast the mean weight of offspring from C mothers is the lowest.

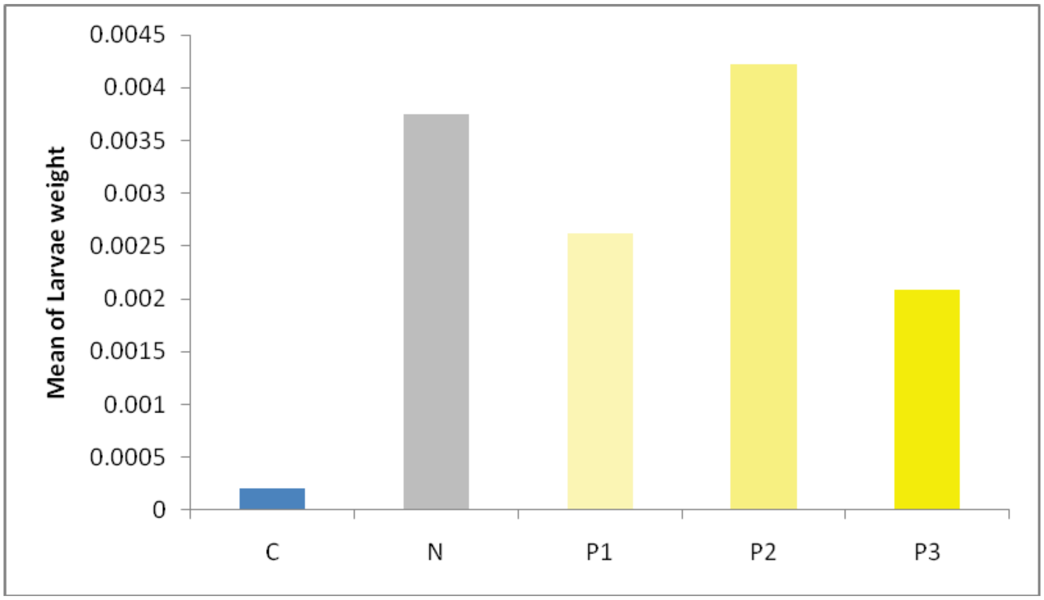


Figure 3: Larval weight for each maternal preference, X axis is mother preference, and Y axis is mean larval weight.

### Offspring performance on each host

Offspring performance is measured as the survival and weight of larvae. There were a total of 400 individuals in the offspring of the 5 categories of maternal preference. Here, I compare the offspring that were fed on *Pedicularis* with offspring that fed on *Collinsia*. Figure 4A shows that, surprisingly, offspring of the more strongly *Pedicularis*-preferring mothers (P2 and P3) achieved higher weights on *Collinsia*.

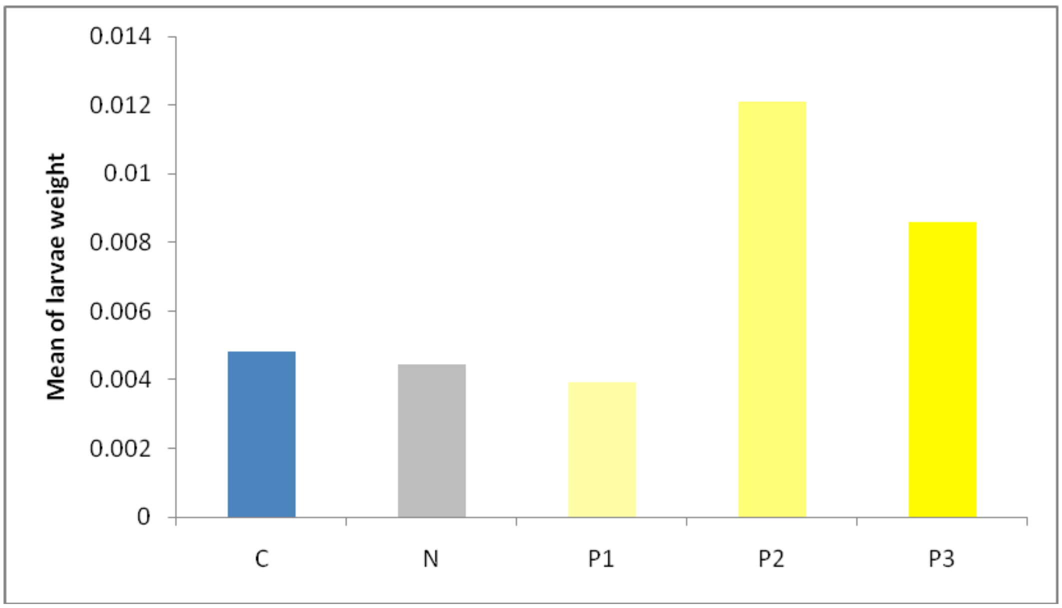


Figure 4A: Larval weight on *Collinsia*

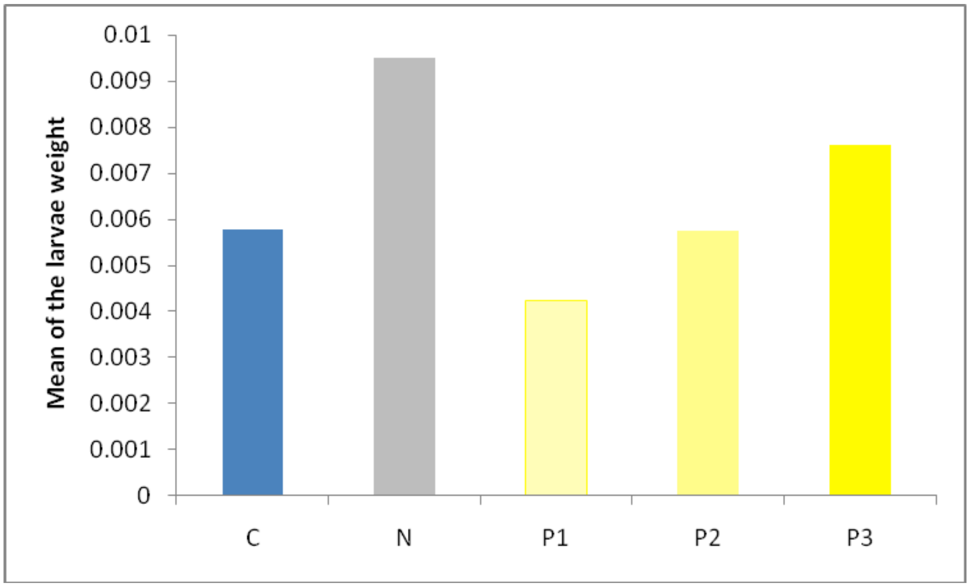


Figure 4B: Larval weights on *Pedicularis*

Figure 4B shows the mean larval weights of larvae fed *Pedicularis*. Again the result was surprising, and not in the direction of the expected preference-performance correlation.

**Larvae survival vs. food**

Figures 5A and 5B show mean survival on *Pedicularis and Collinsia* of larvae from mothers in the five preference categories. Once again, the result seems complex and not clearly in accord with predictions from an adaptive relationship between preference and performance.

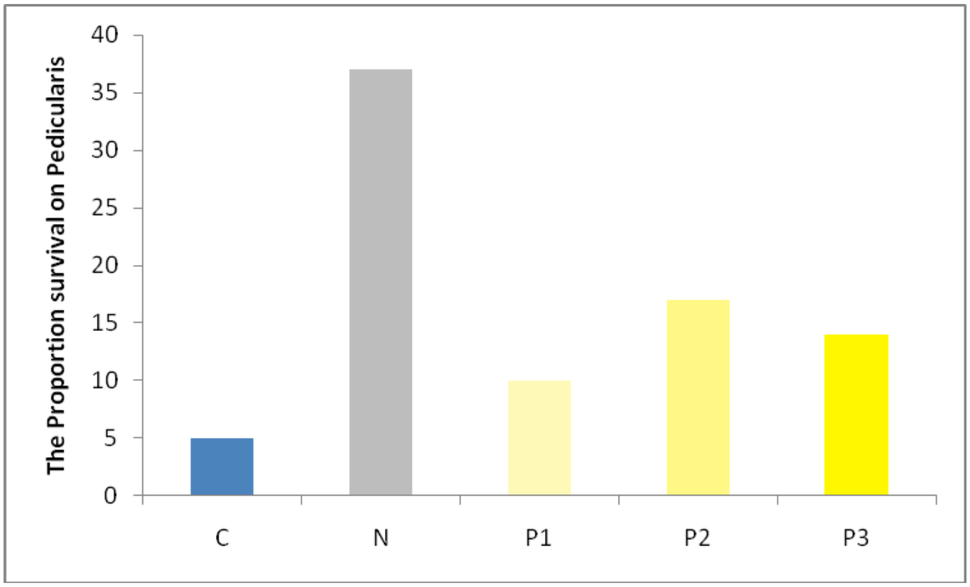


Figure 5A: Survival of individuals that fed on *Pedicularis*

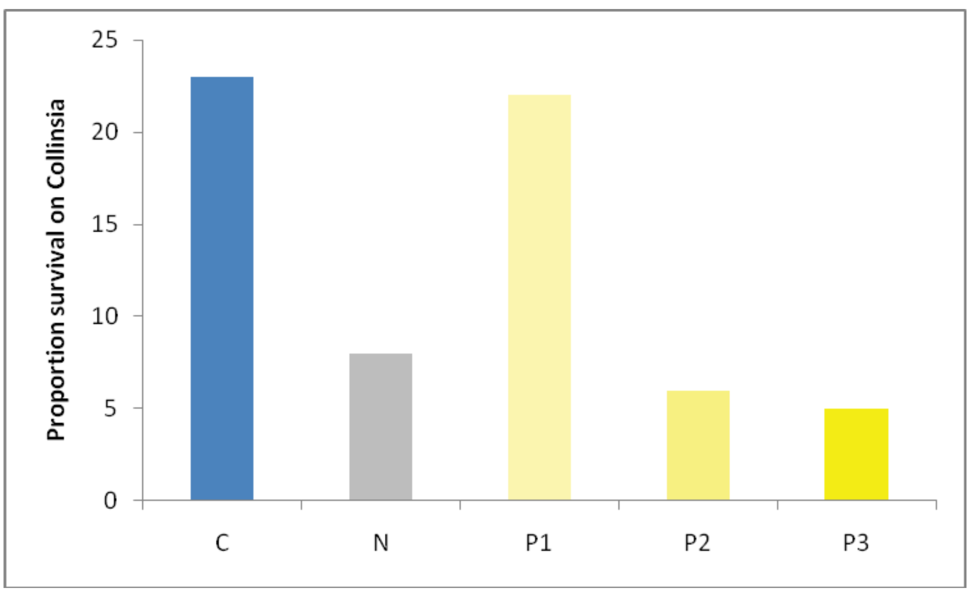


Figure 5B: Survival of individuals that fed on *Collinsia*

# Chapter 5: Conclusion

Maternal oviposition preference of my study butterflies in Rabbit Meadow is quite diverse. Therefore, it would be possible for offspring to show variation of performance in parallel with the very clear variation of maternal preference that I measured. However, they did not. Using different measures of performance, it does seem that there are differences among the offspring of mothers in different preference categories, but these differences do not take the form that would be expected from an adaptive, evolved relationship between preference and performance. The continuing presence of a small percentage of butterflies with clear preference for *Collinsia* seems like a legacy from recent evolution of diet, in which *Collinsia* was included in the diet of thr population following anthropogenic intervention by loggers in the 1960's.

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